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Heat tolerance and physiological plasticity in the Antarctic collembolan, *Cryptopygus antarcticus*, and mite, *Alaskozetes antarcticus*

M.J. Everatt [a],*, P. Convey [b,c], M.R. Worland [b], J.S. Bale [a], S.A.L. Hayward [a]

[a] School of Biosciences, University of Birmingham, Edgbaston, Birmingham B15 2TT, UK
[b] British Antarctic Survey, Natural Environment Research Council, High Cross, Madingley Road, Cambridge, CB3 0ET, UK
[c] National Antarctic Research Center, IPS Building, University Malaya, 50603 Kuala Lumpur, Malaysia

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ABSTRACT

Polar amplification of global warming has led to an average 2 °C rise in air temperatures in parts of the polar regions in the last 50 years. Poikilothermic ectotherms that are found in these regions, such as Collembola and mites, may therefore be put under pressure by changing environmental conditions. However, it has also been suggested that the thermal sensitivity of invertebrates declines with higher latitudes and, therefore, that polar ectotherms may not be at risk. In the current study, the heat tolerance and physiological plasticity to heat stress of two well-studied Antarctic invertebrates, the collembolan, *Cryptopygus antarcticus*, and the mite, *Alaskozetes antarcticus*, were investigated. Both species showed considerable heat tolerance, with each having an Upper Lethal Temperature (ULT) above 35 °C (1 h exposure). These species were also able to survive for over 43 d at 10 °C and for periods of 5–20 min at 40 °C. Across all experimental procedures, *A. antarcticus* possessed a somewhat greater level of heat tolerance than *C. antarcticus*. Water loss during short duration exposures did not differ between the two species at 30, 35 and 40 °C, suggesting that the greater tolerance of *A. antarcticus* over this timescale was not due to higher desiccation resistance. Physiological plasticity was investigated by testing for Rapid Heat Hardening (RHH) and long-term acclimation. RHH was observed to a small degree in both species at a warming rate of 0.5 °C min^{-1}, and also 0.2 °C min^{-1} in *A. antarcticus* alone. Longer-term acclimation (1 week at 10 °C) did not enhance the heat tolerance of either species. Even with this limited physiological plasticity, the results of this study indicate that *C. antarcticus* and *A. antarcticus* have capacity in their heat tolerance to cope with current and future environmental extremes of high temperature.

1. Introduction

Over the last century, the mean surface temperature of the Earth has increased by 0.6 °C (IPCC, 2001). However, the rate of warming has been amplified at higher latitudes, with an average 2 °C rise in parts of the polar regions in the last 50 years (Arctic Council, 2005; Convey et al., 2009; Turner et al., 2009). The northern and western parts of the Antarctic Peninsula have been particularly affected; over the period 1951–2006, data from Vernadsky (Faraday) station in the Argentine Islands recorded a 0.53 °C rise in temperature per decade. A further consequence of this warming at a global scale has been a decrease in snow and ice cover of over 10% since the 1960s (Walther et al., 2002). These trends are set to continue, with general circulation models predicting further warming across the planet, and especially rapid warming in the polar regions.

Invertebrates are poikilothermic ectotherms, meaning that their body temperature is highly influenced by, and varies markedly with, the external environment (Speight et al., 2008). In essence, they are unable to regulate their body temperature as do birds and mammals, and are therefore susceptible to injuries, and developmental and reproductive impairment, resulting from temperature changes (Bale and Hayward, 2010). Invertebrates can respond to these changes through alterations in their behaviour, phenology, physiology and genetic make-up, with these responses acting within or between generations (Lachenicht et al., 2010). Behaviourally, they can track favourable temperatures by moving towards either higher latitudes or altitudes (Walther et al., 2002; Sinclair et al., 2003; Gobbi et al., 2006). Several alpine spiders, for instance, have been shown to remain in their preferred temperature range by tracking the recession of the Forni Glacier in Italy (Gobbi et al., 2006). Invertebrates can also adapt behaviourally on a smaller scale, via microhabitat selection. Habitats, such as the Antarctic fellfields, are host to a diversity of microclimates and invertebrates select those which are the least stressful (Hodkinson et al., 1999; Holmstrup and Zachariassen, 1996; Hoshikawa et al., 1988; Spaull, 1973). Hayward et al. (2000, 2003, 2004) have gone on to show thermal and hygric preferences that are suggestive of this type of behavioural selection in a laboratory setting. A further response identified is a shift of

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* Corresponding author. Tel.: +44 789 620 1770.
E-mail address: mxe746@bham.ac.uk (M.J. Everatt).

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spring and autumn phenology with the changing of the growing season (Ibanez et al., 2010; Walther et al., 2002).

Within generations, physiological adaptation is demonstrated through experimental acclimation or natural acclimatisation—permitting an organism to adapt to changing conditions via a change in form, movement or rate of physiological activity (Lachenicht et al., 2010). In the context of climate change, acclimatisation may involve the improvement of heat tolerance and upper thermal sub-lethal characteristics, such as physical activity, as temperatures rise. This form of adaptation has been shown in a number of organisms, including plants (Meyer and Santarius, 1998), nematodes (Jagdale and Grewal, 2003) and insects (Lachenicht et al., 2010). Over generations, invertebrates can adapt their physiology through the process of natural selection (Somero, 2010).

The thermal sensitivity of terrestrial invertebrates to temperature change has been reported to decline from the tropics to the poles (Addo-Bediako et al., 2000; Deutsch et al., 2008). Some tropical species live very close to their upper thermal limits and, in some cases, at temperatures that exceed their physiological optima (Somero, 2010). Polar species, in contrast, may live chronically below their temperature optima, and are suggested to have sufficient scope to tolerate higher temperatures. Warming might even help to alleviate the stress associated with low temperatures in the polar regions. Climate warming simulation studies using screens, solar domes and other controlled environmental systems (Bokhorst et al., 2008; Bale and Hayward, 2010) suggest a rise in temperature will indeed lead to greater invertebrate numbers in Antarctic communities (Convey et al., 2002; Convey & Wynn-Williams, 2002; Day et al., 2009). However, some manipulation studies also suggest the opposite outcome, with responses depending both on the detailed changes at micro-environmental level associated with the manipulation, and also on the group of invertebrates being considered (Convey et al., 2002, 2003; Bokhorst et al., 2011). Studies into upper thermal thresholds are also used in conjunction with climate manipulation studies and support the view that polar terrestrial invertebrates have low sensitivity to temperature change. Slabber et al. (2007), for example, showed that five Collembola species from a sub-Antarctic island, including *Cryptopygus antarcticus*, possessed Upper Lethal Temperatures (ULT_{50}s) above 30 °C, far higher than the mean summer temperature in the Antarctic.

In the current study, the capacity of the collembolan, *Cryptopygus antarcticus*, and the mite, *Alaskozetes antarcticus*, to tolerate exposure to high temperatures was investigated, and their physiological plasticity to heat stress explored. In particular, this study addressed the ability of each species to respond to rapid increases in temperature, as might occur as a result of solar insolation of their microhabitats during diurnal cycles, and their tolerance to more prolonged exposures to high temperatures based on climate warming predictions. These species were selected as they represent two of the most successful arthropod groups in the maritime Antarctic and are considered 'model' organisms in polar research (Block and Convey, 1995; Block et al., 2009), reaching numbers of up to 1.5×10^6 individuals m^{-2} (Burn, 1986; Convey and Smith, 1997; Tilbrook, 1967). Consequently, any effect warming may have on them will likely be reflected throughout the community.

2. Materials and methods

2.1. Invertebrate collection and storage conditions

Naturally occurring summer-acclimatised individuals of *C. antarcticus* and *A. antarcticus* were collected from algae, moss and rocks on Léonie Island (67°36′S, 68°21′W), near to the British Antarctic Survey's Rothera Research Station, Adelaide Island between January and March 2012. Samples were stored at 4 °C (24:0 L:D) in plastic buckets containing substratum from the site of collection. For water loss experiments (sub-section 2.2.1.), samples were transported to the University of Birmingham under cool conditions (4 °C to 6 °C), taking approximately two months, before being stored at 4 °C (0:24 L:D). All other experiments described were carried out at Rothera Research Station.

2.2. Microhabitat temperatures

The temperature range on Léonie Island on the soil surface underneath a rock was measured between 24 January and 12 March 2012. To illustrate the extremes of temperature potentially experienced by an animal on an exposed surface, temperature was also recorded every 5 min on a rock between 5 and 21 February 2012 at Rothera Research Station, using a Tinytag Transit 2 Datalogger (Gemini Data Loggers, Chichester, UK). Data were uploaded using Tinytag Explorer Software (Gemini Data Loggers, Chichester, UK).

2.3. Upper Lethal Temperatures (ULTs)

The upper temperature at which invertebrates no longer survived was determined by warming individuals of *C. antarcticus* and *A. antarcticus* at 0.2 °C min^{-1} from 4 °C to progressively higher temperatures (30 to 37 °C for *C. antarcticus* and 30 to 40 °C for *A. antarcticus*). Individuals were subsequently held at the target temperature for 1 h, before being cooled back to 4 °C at the same rate. Three replicates of 10 individuals of each species were placed in Eppendorf tubes, which were packed inside glass test tubes plugged with sponge and placed in an alcohol bath (Haake Phoenix II C50P, Fisher Scientific UK Ltd, Loughborough, U.K.) prior to each experimental treatment. Control groups were handled, and exposed, in the same way at 4 °C. The temperature experienced by the invertebrate was measured by placing a thermocouple within an identical Eppendorf tube into one of the glass test tubes. At the end of experimental treatments, individuals were rapidly transferred (over ice) from the Eppendorf tubes into plastic universal tubes containing moist Plaster of Paris, and returned to the rearing conditions (4 °C, 0:24 L:D). Survival, defined by individuals moving either spontaneously or in response to gentle contact stimulus, was assessed 72 h after treatment. Replicate collection, controls, thermocouple use, recovery and survival assessment were the same for all following experimental procedures unless stated otherwise.

2.3.1. Water loss following high temperature exposure

For both species, five replicates of 10 individuals were exposed to three temperatures (30, 35 and 40 °C) as described in sub-Section 2.2. Individuals were weighed prior to and upon removal from each treatment, then following drying to constant mass at 60 °C for 24 h. From these values, initial water content and percentage water loss or gain were calculated (cf. Hayward et al., 2007). The relative humidity was not controlled for during heat exposure.

2.4. Rapid Heat Hardening (RHH)

2.4.1. Determination of the discriminating temperature

In rapid cold and heat hardening experiments the discriminating temperature is defined as the temperature at which there is 10–20% survival after an exposure time of e.g. 1 h (Lee et al., 1987). This temperature was determined here by exposing individuals (three replicates of 10 individuals) of *C. antarcticus* and *A. antarcticus* directly (i.e. without ramping from 4 °C) to